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Facultative sex ratio bias in the offspring of Seychelles warblers

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SUMMARY

Young Seychelles warblers (*Acrocephalus sechellensis*) frequently remain in their natal territories as helpers. Helpers on low-quality territories (as measured by food availability) reduce their parents' future reproductive success, whereas helpers on high-quality territories increase their parents' future reproductive success, thereby improving their own indirect component of inclusive fitness. Helpers are mainly females, which remain longer in their natal territories than males. The Seychelles warbler shows extreme skews in sex ratios of offspring at six months of age, varying from mainly males on low-quality territories to mainly females on high-quality territories. It appears that breeding birds avoid having helpers on low-quality territories and gain helpers on high-quality territories, thereby increasing their reproductive success. There is evidence that the biased sex ratio is caused by biased production, and not because of biased mortality at younger ages: (i) cumulative mortality from the egg stage to the stage at six months of age is insufficient to generate a consistent deviation from sex ratio parity; (ii) all 30 nestlings produced by two pairs on low-quality territories survived to be sexed as sons, and all nestlings produced by two pairs on high-quality territories survived to be sexed as 17 daughters and one son; and (iii) in addition, breeding pairs that were transferred from low- to high-quality territories, switched from the production of male to female nestlings.

1. INTRODUCTION

Trivers & Willard (1973) argued that, in species with parental care, it may be profitable for parents to skew the sex ratio of their offspring to maximize their own fitness. Skewed sex ratios are predicted when the profitabilities of raising sons and daughters in terms of fitness vary predictably in the population (Trivers & Willard 1973; Clutton-Brock 1986). Evidence for the adaptive nature of inter-individual sex ratio variation in birds has been presented only for the kestrel (*Falco tinnunculus*). In this species, the seasonal decrease in the proportion of male offspring is adaptive because of the seasonal decline in the probability that males (but not females) breed at 1 year of age (Dijkstra *et al.* 1990). Another factor that may affect optimal sex ratios is the likelihood of 'helping' by one sex of offspring in cooperative species (Gowaty & Lennartz 1985; Emlen *et al.* 1986; Lessells & Avery 1987). If offspring of one sex help their parents, thereby enhancing the fitness of their parents (local resource enhancement (LRE)), it may be more valuable for the parents to invest in the helping sex than in the non-helping sex. However, if offspring of one sex compete with their parents for local resources (local resource competition (LRC)), it may be more valuable for the parents to invest in the dispersing, non-helping sex (Clutton-Brock & Iason 1986; Johnson 1988). In this paper I address sex ratio

in relation to both LRE and LRC using data from the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*).

The Seychelles warbler is a rare endemic, known only from the Seychelles Islands. Until 1988, it occurred only on Cousin Island (29 ha), but additional breeding populations were successfully established on the islands of Aride (68 ha) and Cousine (26 ha) in September 1988 and June 1990, respectively (Komdeur *et al.* 1991; Komdeur 1994*a*). The normal clutch size of the warbler is one egg (91.0%, $n = 223$). The breeding pair may remain together in the same territory, for as long as 9 years (Komdeur 1992, 1996*a*). Although Seychelles warblers can breed successfully in their first year, some individuals remain on their natal territories as helpers. Helpers of both sexes aid in territory defence, predator mobbing, nest-building (mainly females), incubation (females only), nest guarding (mainly males) and feeding of dependent young which are probably not their own offspring (Komdeur 1994*b*). Helpers which did not care for the young in the nest never began acting as helpers after the young fledged ($n = 161$; Komdeur 1991). Both territory quality and the presence of helpers are important factors affecting the fitness of parents. Breeding pairs that were transferred from low- to high-quality territories improved their reproductive success significantly (Komdeur 1996*b*). Removal experiments showed that the presence of helpers in high-quality territories improved the reproductive success of their parents, because of helping behaviour (LRE), while the

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presence of helpers on low-quality territories decreased future reproductive output of their parents, because of competition for food and breeding (LRC) (Komdeur 1994*b*). To improve reproductive success, parents in high-quality territories would favour helpers among their offspring, and parents in low-quality territories non-helping, dispersing offspring.

This study was designed to answer two questions. First, are delayed dispersal and helping behaviour sex specific? Second, if so, do Seychelles warblers manipulate the sex ratio of their offspring in an adaptive fashion? I use 14 years of data from a genealogically known population. For some breeding pairs, the exact offspring sex ratio at hatching is known throughout their breeding lives. The transfers of Seychelles warbler pairs from low-quality territories on Cousin Island to high-quality territories on the previously unoccupied islands of Aride and Cousine, allowed me to compare the production of potential helpers by the same pairs pre- and post-transfer.

2. MATERIALS AND METHODS

(a) Data collection

The entire population of Seychelles warblers on Cousin Island (115–123 groups, 310–400 birds) was under study between December 1985 and August 1995. Data presented here were based on individually colour-ringed birds. All territories were checked fortnightly for nests with an egg or young and for the presence of colour-ringed birds to determine the proportion of birds that survived. Once a bird was missing from its territory, all other territories were checked to assess dispersal. As Seychelles warblers have never colonized other islands by themselves, I assumed that missing birds had died if they were not found on other territories. Food provisioning observations were made for 3 h comprising three sessions of 1 h equally spaced over the day: 06h30–10h30, 10h30–14h30 and 14h30–18h30. Feeding observations started in the second week after hatching and were repeated every 3 weeks until young died or reached independence. For each half-minute it was noted whether or not each bird was feeding the young. Total food provision frequency to fledglings throughout the period of dependence was measured as the summation of mean food provision rates per 3-week intervals after fledging. All nestlings were individually colour-ringed, and as many as possible were weighed at day 19 (fledging), in the third and in the sixth month after hatching.

(b) Sex determination

Offspring sex ratios were based on observations of birds at 6 months of age. Warblers younger than half year of age could not be sexed by measurements, because biometrics were the same for both sexes (Komdeur 1991). When older than half year of age, males are significantly heavier, and have significantly longer wings and tarsi than females (Komdeur 1991). All surviving individuals colour-ringed as nestlings were caught at six months of age and sexed by these measurements. All males ($n = 23$) and females ($n = 32$) sexed at 6 months of age and seen copulating at a later stage were correctly sexed.

(c) Territory quality

Territory quality, independent of the presence of nest sites and nest predators (Komdeur 1991, 1994*a, b*), was measured

in terms of insect prey available, because this correlated with adult survival and reproductive success (Komdeur 1991). As the warblers are insectivorous, territory quality (TQ) was expressed as mean number of prey invertebrates available within a territory (for method, see Komdeur 1991, 1994*b*). I measured the quality of territories each month. As the quality of breeding territories remained constant between years (Komdeur 1996*a, b*), territory quality was expressed as the average quality over the whole research period. Territories were divided into three categories (prey invertebrates/100): low (TQ = 0–15), medium (TQ = 15.1–30), and high quality (TQ > 30).

(d) Removal experiment

The translocation of Seychelles warblers, and the fact that birds of seven breeding pairs from Cousin remained together on the new islands, enabled me to measure the influence of territory quality on offspring sex ratio by comparing pre- and post-transfer offspring sex ratios for each pair. A total of four breeding pairs from low-quality territories and three breeding pairs from high-quality territories were transferred. On the new islands these pairs all occupied high-quality territories. The offspring sex ratio of each pair was exactly known for the 3 years before and 2 years after the translocation to Aride, and in the 5 years before and 17 months after translocation to Cousine.

(e) Data analyses

Helping data were based on observations of feeding young at the nest. Only those potential helpers were considered, whose putative parents were still alive, because kin discrimination in helping exists (Komdeur 1994*c*). In this analysis data were pooled over 5 years of study (1986–1990), and only one randomly selected age category for each bird was used. To quantify how helping varied with age, only those birds were included which had an opportunity to help, i.e. those where a nest with young was present in their natal territories. The factors which may affect helping behaviour were analysed by stepwise forward logistic regression. A variable enters into the equation only if the probability (p) associated with the G -test on the decrease in scaled deviance ($'D'$) is less than 0.05.

Tests on territory quality related offspring sex ratio were based on total young produced and on the first young produced for each breeding pair. This was because the sex ratio of offspring could be dependent on the presence or absence of older offspring (Gowaty & Lennartz 1985; Komdeur 1992). The possible effects of clutch size on sex ratio variation were controlled for by only considering nests containing one egg. Tests on territory-quality related offspring dispersal were based on one randomly selected offspring for each breeding pair, and tests on age-related helping activity were based on one randomly selected age category for each potential helper to avoid pseudoreplication.

Unless stated otherwise, means are expressed with standard deviations, probability values are two-tailed, and the null hypothesis was rejected at $p < 0.05$.

3. RESULTS

(a) Territory quality and dispersal

The minimum and maximum age at which birds left their natal territories were 10 and 97 months for females, and 6 and 34 months for males, respectively. The higher the quality of a territory, the longer young remained in territories there (figure 1). In addition,

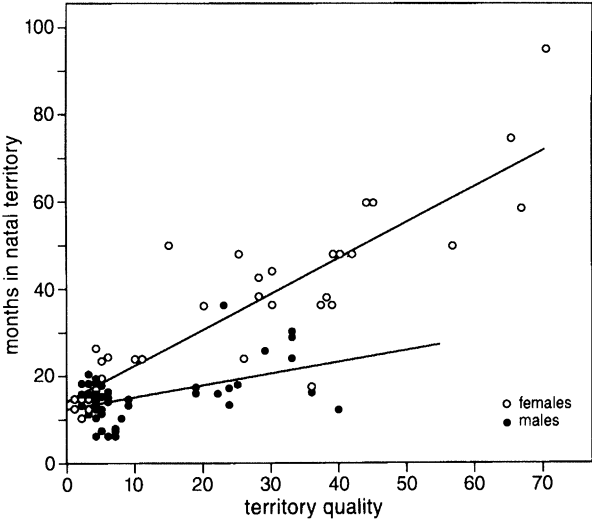


Figure 1. Effect of territory quality upon length of period remaining in natal territories by Seychelles warbler female and male offspring (females: months in natal territory = $0.83 \times \text{TQ} + 13.87$, $r^2 = 0.77$, $n = 39$, $p < 0.001$; males: months in natal territory = $0.28 \times \text{TQ} + 12.17$, $r^2 = 0.27$, $n = 54$, $p < 0.001$). The slopes of the two regression lines are significantly different ($t = 16.97$, d.f. = 91, $p < 0.001$).

Table 1. Sex of helpers among Seychelles warblers (1986–1995)

(The frequency of male and female helpers significantly differed from equality (binomial test: $p < 0.001$).)

year	number of helpers		
	males	females	total
1986	6	65	71
1987	3	41	44
1988	3	19	22
1989	4	18	22
1990	5	20	25
1991	2	16	18
1992	2	14	16
1993	3	14	17
1994	1	8	9
1995	5	22	27
total	34	237	271

females remained significantly longer in their natal territories than males (figure 1).

(b) Sex and age of helpers

In all the years during the research period female helpers predominated significantly (table 1): of all helpers, 88% were females. The fraction of non-breeding birds that helped increased with age of the bird (see figure 2). During the first year of age, the fraction of birds becoming helpers was low, and was equal for males and females. During the second and subsequent years of age, relatively more females than males were helpers. Age explained most of the variance in fraction of birds helping ($D = 87.21$, d.f. = 1, $p < 0.001$). After controlling for age, the quality of the natal territory was of significant effect ($D = 6.19$, d.f. = 1, $p = 0.01$), and after controlling for age and

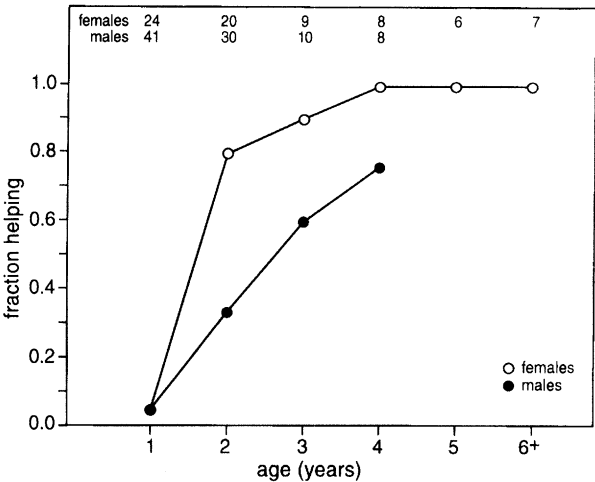


Figure 2. Fraction of young helping feeding nestlings at different ages in female and male Seychelles warblers, which were still in their natal territories. Only one randomly selected age category for each bird was used. Top figures are number of females and number of males which could have been helpers at a certain age, because nests with young were present ($n = 163$ individuals, 74 females and 89 males).

territory quality effects, the gender of bird significantly affected the probability of helping ($D = 7.23$, d.f. = 1, $p = 0.01$).

(c) Territory quality and offspring sex ratio

The facts that helpers were mainly females, and that helping occurred much more on high-quality territories, suggest that pairs in high-quality territories might gain fitness benefits from female offspring. These daughters would become helpers in later years and breeding pairs may thereby enhance their reproductive success. Conversely, pairs in low-quality territories might favour dispersing male offspring, thus avoiding, paradoxically detrimental, helpers and possibly a lower future reproductive success.

There is, indeed evidence that the sex ratio of young correlates with territory quality (see figure 3). The fraction of total female offspring present in the population significantly increased from 0.16 in low-quality territories to 0.68 in high-quality territories. Most offspring in low-quality territories were males (76.9%, $n = 212$), neither male nor female offspring predominated significantly in medium-quality territories (46.9% males, $n = 64$), and offspring in high-quality territories were mainly females (65.4%, $n = 104$). If only considering the first young produced by the breeding pairs, then the fraction of female offspring significantly changed from 0.22 to 1 with increasing territory quality (figure 3). Most offspring in low-quality territories were males (74.6%, $n = 110$), neither male nor female offspring predominated significantly in medium-quality territories (55.2% females, $n = 29$), and offspring in high-quality territories were mainly females (87.2%, $n = 39$). The fraction of total female offspring on high-quality territories was significantly less than the fraction of females in the first young raised in these territories ($\chi^2 = 5.57$, d.f. = 1, $p < 0.025$).

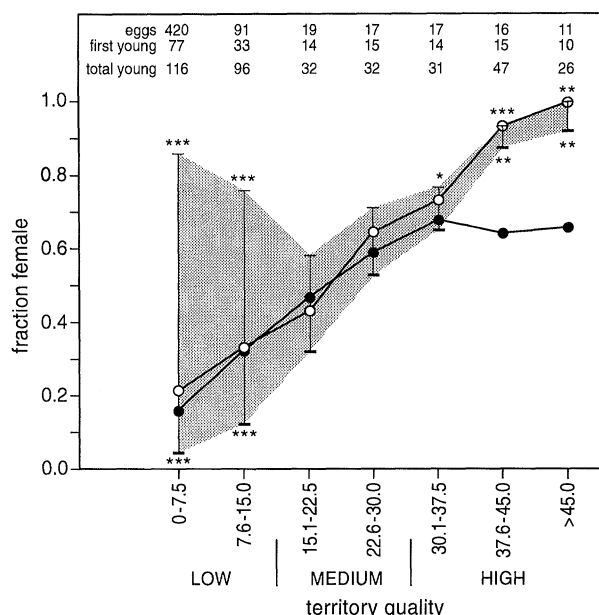


Figure 3. Offspring sex ratio in Seychelles warblers measured at the age of 6 months in relation to quality of breeding territory. Offspring sex ratio is based on total young present in the population (filled dots) and on the first young produced by the breeding pairs with no additional birds present on the territory (open dots). Young were hatched from one-egg clutches only (total young: $n = 380$, G -test of independence: $D = 67.97$, d.f. = 2, $p < 0.001$; fraction female = $1/(1 + e^{-z})$; $z = 2.195 - 0.148 \cdot \text{tq} + 0.002 \cdot \text{tq}^2$; first young: $n = 178$; $D = 53.13$, d.f. = 1, $p < 0.001$; $z = -1.613 + 0.082 \cdot \text{tq}$). Top numbers are number of 6-months-old young. The predicted offspring sex ratio at age of 6 months by breeding pairs without additional birds present on the territory is also plotted, which was measured under the assumption that all the eggs that did not hatch were males (thick dash at the end of bar from open dot) or were females (thin dash at the end of bar from open dot) ($n = 591$ eggs; top figures are number of eggs with known fraction resulting in 6-months-old young; binomial test: $*p < 0.05$, $**p < 0.025$, $***p < 0.001$).

The shift from male bias in low-quality territories to female bias in high-quality territories is potentially caused by either a change in primary sex ratio (of the eggs) or in sex-specific survival from the egg stage to the stage at which young reach half year of age, or both. I investigated sex ratio variations in a sample of 591 eggs laid by breeding pairs without additional birds present on the territory, and with known fraction resulting in half year old young. Even if I assume that all the eggs that did not hatch were males, a significant increase in female offspring with territory quality still remains (figure 3). The offspring sex ratio in territories with a quality less than 15 was significantly biased towards males, and on territories of quality greater than 37.7 significantly towards females. If I assume that all the eggs that did not hatch were females, then pairs in territories with a quality less than 15 or greater than 30 produced significantly more females (figure 3). Thus, the greater uncertainty in possible error in estimation of offspring sex ratios for low-quality territories is a result of a higher nest failure rate.

For five breeding pairs all nestlings produced between 1985 and 1995 were colour-ringed and all

survived to be sexed at 6 months of age. All offspring produced by the two pairs on low-quality territories were males (binomial-test, $n = 9$, $p = 0.004$, and $n = 21$, $p = 0$, respectively). Of the offspring produced by one pair on medium-quality territory, 46% were males ($n = 11$, $p = 1$). Of the offspring produced by two pairs on high-quality territories all, respectively, 89% were females ($n = 9$, $p = 0.004$, and $n = 9$, $p = 0.039$, respectively). On these territories no apparent weight differences existed among male and female offspring at fledging (at 19 days) and at reaching independence (3 months) (mean fledging weight (gr) male versus female (s.d., n): 16.2 (0.91, 36) versus 16.1 (0.88, 23); $t = 0.38$, d.f. = 57, ns); mean weight at 3 months of age: 15.7 (0.81, 36) versus 15.7 (0.86, 23); $t = 0.14$, d.f. = 57, ns). Mean food provision frequency to nestlings and mean total food provision frequency to fledglings throughout the period of dependence by warbler pairs on these territories was the same to female offspring as to male offspring (mean food provision rate (per hour) to male versus female nestling (s.d., n): 25.4 (3.8, 36) versus 24.3 (2.3, 23); $t = 1.25$, d.f. = 57, ns); mean total food provision rate (per hour) to male versus female fledgling: 52.4 (7.9, 36) versus 55.5 (8.6, 23); $t = 1.41$, d.f. = 57, ns).

(d) Within-pair comparison of offspring sex ratio before and after transfer

Breeding pairs that were transferred from low-quality territories on Cousin to high-quality territories on the new islands, switched from an offspring sex ratio biased towards sons before the transfer to mainly daughters after the transfer (table 2). Offspring sex ratios of pairs breeding on high-quality territories before and after translocation were biased towards females during both periods (table 2).

4. DISCUSSION

(a) Facultative offspring sex ratio variation

Offspring sex ratio bias is a rare event among birds. Significantly female-biased sex ratios at hatching have only been reported in the green woodhoopoe (*Phoeniculus purpureus*; Ligon & Ligon 1990), and male-biased sex ratios at fledging have only been reported in the red-cockaded woodpecker (*Picoides borealis*; Gowaty & Lennartz 1985), in the Harris' hawk (*Parabuteo unicinctus*; Bednarz & Hayden 1991), and in the marsh harrier (*Circus aeruginosus*; Zijlstra *et al.* 1992). Seasonal decline in nestling sex ratios have been reported in the kestrel (Dijkstra *et al.* 1990), and seasonal increase of secondary sex ratio has been reported for the common grackle (*Quiscalus quisicalus*; Howe 1977). A decline in sex ratio with egg sequence is known in ring-billed gulls (*Larus delawarensis*; Ryder 1983) and kestrels (Dijkstra *et al.* 1990).

It is well established, both theoretically (Trivers & Willard 1973) and empirically (Clutton-Brock *et al.* 1981; Clutton-Brock *et al.* 1984), that in populations of polygynous animals those parents living in the best condition may invest more in their sons than in their daughters, because the breeding success of males is

Table 2. Comparison of offspring sex ratio and territory quality of Seychelles warbler pairs on Cousin Island before translocation, and on the islands of Aride and Cousine after translocation (significances assessed using χ^2 tests)

(The change in offspring sex ratios from low- to high-quality territories was significant ($\chi^2 = 26.20$, d.f. = 1, $p < 0.001$), but that from high- to high-quality territories not ($\chi^2 = 0.10$, d.f. = 1, $p = 0.79$).)

Tq pair	pre-removal			post-removal		
	low daughters	sons	χ^2 (d.f. = 3)	high daughters	son	χ^2 (d.f. = 3)
1	0	6	13.9 ^b	12	0	18.76 ^c
2	1	2		3	1	
3	1	6		9	2	
4	0	4		5	2	
total	2	18		29	5	
Tq pair	high daughters	sons	χ^2 (d.f. = 2)	high daughters	sons	χ^2 (d.f. = 2)
5	4	1	6.47 ^a	2	1	8.11 ^b
6	6	2		8	1	
7	5	1		6	2	
total	15	4		16	4	

^a $p < 0.05$.
^b $p < 0.025$.
^c $p < 0.001$.

more variable than that of females. However, another way to increase the fitness of parents in cooperatively breeding species is to produce helpers when these are needed. In the Seychelles warbler, parents living in high-quality territories produce more daughters. Benefits of this strategy do not seem to be based on variable breeding success of males (Komdeur 1991), but on increased future reproduction of the parents.

The higher the food availability on the parental territory, the longer young Seychelles warblers delayed their dispersal. Helpers were mainly females, which remained significantly longer in their natal territories than males. Especially for females, the gain of helping experience translates into improved reproductive success when a helper becomes a breeder (Komdeur 1996c). In contrast to the small variations in offspring sex ratios that seem to characterize birds (Williams 1979; Gowaty & Lennartz 1985; Gowaty 1991), the Seychelles warbler on Cousin Island shows very strong skews in offspring sex ratios. This sex ratio bias was neither influenced by social circumstances (no additional birds were present on the breeding territories) nor by clutch size (in the analyses only clutches of one egg were included).

The sex ratio variation in Seychelles warblers offers support for the ‘production-of-helpers’ hypothesis (Gowaty & Lennartz 1985; Emlen *et al.* 1986; Lessells & Avery 1987). It is further consistent with the local resource competition and local resource enhancement hypotheses. By biasing offspring sex ratio towards male sex in low-quality territories and female-sex in high quality territories: breeding birds avoid having competing offspring on low-quality territories (LRC), and gain helpers on high-quality territories (LRE). It seems that breeding pairs have developed an adaptive behaviour to increase their reproductive success. Offspring sex ratio based on the first 6 months old young produced by warbler pairs without additional

birds on high-quality territories was significantly more female biased than offspring sex ratio based on total offspring produced by pairs on high-quality territories with additional birds present. With more helping birds present in a high-quality territory, the reproductive success of the parents decreases, resulting from the greater depletion of food resources (Komdeur 1994b). Under these circumstances it may pay to produce more dispersing sons. These results support the general proposition of Trivers & Willard (1973) that sex ratio variation is expected when the profitabilities of raising sons or daughters vary between individuals. Apart from the kestrel (Dijkstra *et al.* 1990) and the Seychelles warbler, I know of no empirical and experimental demonstration in birds that the sex ratio distribution actually results in an increased future reproductive success for the parents. The translocation of breeding pairs from low-to-high quality territories was associated with a significant switch from male biased offspring to female biased offspring. This experiment showed that Seychelles warblers manipulate their offspring sex ratio facultatively, depending on food availability.

(b) Mechanisms of facultative sex ratio manipulation

The data presented here suggest that the biased sex ratio is caused by biased production rather than mortality. This is based on three observations.

1. On Cousin Island, the offspring bias towards females on territories with high quality was not caused by sexual differential mortality from the egg stage to the stage at which young reach the age of 6 months. In addition, sex ratio of hatchlings was significantly biased towards males in two breeding groups on low-quality territories, and towards females in two breeding groups on high-quality territories. Breeding pairs, that were experimentally transferred from low- to high-quality

territories, switched from the production of male to female offspring. These data thus indicate that the territory quality dependence of the sex ratio reflects systematic variations in the primary sex ratio of the eggs as laid.

2. Support for a systematic variation in nestling sex ratio determined before egg laying (primary sex ratio bias) also comes from the warblers breeding on high-quality territories on the new islands. All but one of the eggs hatched ($n = 59$) and all these nestlings survived to be sexed at the age of 6 months. Hatchlings produced in these territories were significantly biased towards females (84.8%).

3. According to Fisher's (1930) theory, a surplus of male offspring would be predicted if the parental investment in a son were less than that in a daughter. In the Seychelles warbler, there is no reason to hypothesize cost differential between sons and daughters, as warblers younger than 6 months have no sexual size dimorphism which may suggest sex differences in energy requirements. These similar weights at similar ages for each sex were not caused by differential mortality or by differential feeding by the parents.

Therefore, the most plausible current interpretation of the facts is that Seychelles warblers are able to adjust the sex of their eggs to the quality of the territory they inhabit. Although the long-term fitness benefits of the sex ratio strategies remain to be observed, it is likely that pairs in high-quality territories benefit from the help of daughters, and pairs in low-quality territories benefit from dispersing sons. I need to await techniques for sexing eggs or hatchlings to assess whether the adjustment is done at egg production.

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